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Potential role of Collembola as biotic mortality agents for entomopathogenic Nematodes

S. K. Gilmore[1] **and D. A. Potter**[2]

[1] Alice Lloyd College, Pippa Passes, Kentucky, U.S.A.
[2] Department of Entomology, University of Kentucky, Lexington, Kentucky, U.S.A.

Summary. The capacity for the collembolans *Folsomia candida* (Isotomidae) and *Sinella caeca* (Entomobryidae) to consume three species of entomopathogenic steinernematid nematodes and to reduce the effectiveness of nematode applications against larvae of the wax moth, *Galleria mellonella* (Pyralidae) and Japanese beetle, *Popillia japonica* (Scarabaeidae) was studied in the laboratory. Both collembolans readily consumed large numbers of nematodes. Phoresy or adverse effects of nematodes on Collembola were not observed. Mortality of wax moth larvae caused by *Steinernema carpocapsae* declined markedly as the time of prior exposure of the nematodes to collembolan predation increased. As few as five *F. candida* added to chambers containing 100 or 200 *S. carpocapsae* caused significant reductions in nematode-induced mortality of *G. mellonella* within 24 h. In contrast, presence of Collembola did not reduce the efficacy of nematodes against *P. japonica* grubs in turfgrass plugs. Collembolan predation may be more likely to reduce the effectiveness of nematode applications against surface-feeding insects than against subterranean root-feeders.

Key words: Collembola, Steinernematidae, Scarabaeidae, Turfgrass, Biological Control

Introduction

Development of techniques for mass rearing, storage, and shipment of entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae (Gaugler & Kaya, 1990) has increased their versatility for biological control of soil-inhabiting insects. Scarabaeid larvae, corn rootworms, flea beetles, root weevils, mole crickets, and cutworms are among those soil inhabiting insect pests whose potential control has been investigated (Klein, 1990) Turfgrass-infesting insects are one group against which the potential for successful control has been demonstrated (Shetlar et al., 1988; Villani & Wright, 1988).
Environmental factors are known to affect the efficacy of entomopathogenic nematodes for biological control (Georgis & Gaugler, 1991). Nematode survival is affected by temperature (Boivin & Belair, 1989) and moisture content at the time of application or thereafter (Shetlar et al., 1988; Georgis & Gaugler 1991). Soil texture affects the ability of nematodes to penetrate or move through soil to locate potential hosts (Georgis & Poinar, 1983a, b). The unpredictability of field applications is a significant obstacle to expanding the use of nematodes beyond their present application in small-niche markets against soil-inhabiting pests of citrus, cranberris, ornamentals, and turf (Georgis & Gaugler, 1991).

Correspondence to: Samuel K. Gilmore

Nematophagous microarthropods may also reduce the number of nematodes reaching and infecting target pests. For example, Epsky et al. (1988) observed that twelve species of soil-inhabiting mites fed upon infective stage juveniles of *Steinernema carpocapsae* (Weiser) and *Heterorhabditis bacteriophora* Poinar (= *H. heliothidis* Khan, Brooks, and Hirschmann) in the laboratory, and showed that predation by one species, *Gamasellodes vermivorax* Walter (Mesostigmata: Ascidae), was great enough to reduce efficacy of nematodes against greater wax moth, *Galleria mellonella* (L.) (Pyralidae) prepupae. Many of the mite species also served as phoretic hosts for *S. carpocapsae*, after which the nematodes were found to be still infective (Epsky et al. 1988).

Collembola are prominent members of most soil invertebrate communities, being second only to mites in numbers (Hale, 1967; Wallwork, 1974). Collembola are generally regarded as omnivorous, feeding on decaying organic matter, fungi, yeasts, and other foods (Christiansen, 1964; Gilmore & Raffensperger, 1970; Wallwork, 1974). Gilmore (1970) demonstrated that several collembolan species will consume large numbers of bacteria-feeding, fungivorous, and plant-parasitic nematodes, and will grow more rapidly on a diet of nematodes than on a standard laboratory diet of dried baker's yeast. Similarly, Epsky et al. (1988) observed that the collembolan *Hypogastrura scotii* Yosii (Hypogastruridae) consumed *S. carpocapsae* and could complete its development on infective stage nematodes.

Because of their abundance in most soil habitats, including turfgrass soils, and because of the avidity with which they consume nematodes, we hypothesized that Collembola could consume enough infective stage juveniles to reduce the efficacy of entomopathogenic nematodes in biological control. The objective of this study was to measure the capacity for two collembolan species to consume three species of entomopathogenic nematodes, and to determine if collembolan predation could reduce the effectiveness of nematode applications against either wax moth larvae, which were used as a standard bioassay (Woodring & Kaya, 1988), or Japanese beetle, *Popillia japonica* (Scarabaeidae) larvae in the laboratory.

Materials and Methods

Entomopathogenic nematodes were obtained from Biosys Corp., (Palo Alto, Calif., U.S.A.). *Steinernema carpocapsae* (All strain) was used in tests involving wax moth larvae; *S. carpocapsae* and *S. glaseri* (Steiner) (Strain 22) were used for assays with Japanese beetle grubs, and these two species plus *S. feltiae* (Strain 27) were used in feeding trials. *Steinernema carpocapsae* and *S. feltiae* were shipped to us suspended in polymer gel in the commercial formulation Biosafe®, stored at 3 °C, and suspended in water according to label directions before use. *Steinernema glaseri*, which was not commercially available at the time of this study, was shipped in water and stored at 8 °C until use (5 days after arrival).

Concentrations of nematodes in the suspensions of *S. carpocapsae* or *S. feltiae* as prepared above, and in the original shipment of *S. glaseri*, were determined by averaging counts from five samples prepared by mixing 1 ml of the original suspension in 500 ml of water. From each of the five samples, three 1 ml subsamples were transferred to counting dishes consisting of a plastic petri dish (60 mm diam.) with a 2 mm grid. Enough water was added to cover the bottom of the dish so that the nematodes would be evenly spread. At each transfer the total suspension was mixed with a magnetic stirrer and the samples taken from the same spot in the container. After determining the original concentration from the average of the 15 counts, an appropriate portion of the original suspension was transferred to another container and diluted to achieve the desired concentration for use in bioassays. All nematode numbers reported herein are approximates, as estimated from such dilutions.

Wax moth larvae were obtained from Grubco, Inc., Hamilton, Ohio, and stored at 3 °C until used. Third instar Japanese beetle grubs were dug from beneath Kentucky bluegrass (*Poa pratensis* L.) turf at the University of Kentucky Spindletop Research Farm, Lexington, Ky., and stored in moist soil at 10 °C for 1–2 days until used in assays.

Two species of Collembola, *Folsomia candida* Willem (Isotomidae) and *Sinella caeca* (Schott) (Entomobryidae) were obtained from a pile of leaf litter on the campus of Alice Lloyd College, Pippa

Passes, Ky. Cultures were maintained as described by Gilmore (1970) and fed dry baker's yeast. Adult or subadult specimens, based on size, were selected from cultures for use in feeding trials.
Most trials were conducted in chambers consisting of covered plastic petri dishes (100 mm diam.) with a 2 mm layer of charcoal-plaster of Paris (C-PP; 1 : 9 dry volume). Since it was determined that individual chambers could absorb about 7 to 8 ml of water, the C-PP was first moistened with 5 ml of water, followed by a 1 or 2 ml sample of nematode suspension. The number of nematodes remaining in a chamber after an assay was determined by rinsing the lid of the dish into the bottom, rinsing the bottom five times with each rinse being poured into the counting dish, and then counting any nematodes present.

Consumption of Nematodes by Collembola

The capacity for each of the collembolan species to consume entomopathogenic nematodes was tested in four trials involving nine separate combinations of Collembola, nematodes, and durations of exposure. Numbers and species of Collembola used, and duration of each assay are indicate in Table 1. Five replicates were prepared of each treatment. There initially were an estimated 300 infective-stage juvenile nematodes per chamber in Trials 1—3, and about 500 nematodes per chamber in Trial 4. Chambers were kept in the dark at room temperature (about 22 °C) for 3 to 9 days, after which the nematodes remaining were counted and compared to the number remaining in identical chambers with the same initial number of nematodes, but without Collembola.

Tests for Phoresy of Nematodes on Collembola

Epsky et al. observed mites serving as phoretic hosts for *S. carpocapsae*. Although we did not directly observe nematode phoresy on Collembola in any assay, several tests were conducted to determine if the Collembola might serve as phoretic hosts in a way that hid the nematodes.
Folsomia candida were confined with *S. carpocapsae* in the manner described for the consumption trials. There were five replicates, each with 20 Collembola and an estimated 300 nematodes. After 6 days the Collembola from each replicate were transferred to separate jars (20 ml) containing water and vigorously shaken. The water was then transferred to counting dishes and examined for presence of live nematodes.
Another, more extensive test involved preparation of five replicates of each of the following combinations: 1) 20 *F. candida* which had been exposed to 300 *S. carpocapsae* for 6 days in the

Table 1. Consumption of entomopathogenic nematodes by two species of Collembola in feeding chambers

Trial	Nematode Species	Collembola (no./chamber)	Days of exposure	Mean (± SE) nematodes recovered[1]	
				Without Collembola	With Collembola
1	*Steinernema carpocapsae*	*Folsomia candida* (20)	3	197 ± 8.1	4.8 ± 1.4**
	Steinernema carpocapsae	*Folsomia candida*	6	186 ± 9.5	3.8 ± 1.1**
2	*S. carpocapsae*	*Sinella caeca* (20)	3	210 ± 9.3	2.6 ± 1.3**
3	*S. feltiae*	*F. candida* (20)	9	196 ± 30.9	0.3 ± 0.3**
4	*S. glaseri*	*F. candida* (10)	7	473 ± 26.1	433 ± 43
	S. glaseri	*F. candida* (20)	7	—	353 ± 29*
	S. glaseri	*F. candida* (50)	7		259 ± 16*
	S. glaseri	*S. caeca* (10)	7	—	230 ± 12*
	S. glaseri	*S. caeca* (20)	7	—	76 ± 17*

** Denotes significant difference from corresponding control; $P < 0.001$; two-sample t-test
* Within Trial 4, means marked by an asterisk differ significantly from control mean (without Collembola); $P < 0.05$; Dunnett's test for treatments vs. control

aforementioned manner were transferred to fresh experimental chambers, to which ten *Galleria* larvae were then added; 2) 20 *F. candida* were confined with 300 *S. carpocapsae* for 6 days, afte which then *Galleria* larvae were added to the same chambers; 3) 10 *Galleria* larvae were added to chambers that had been inoculated with 300 *S. carpocapsae*, but no Collembola, 6 days earlier; and 4) 10 *Galleria* were added to fresh experimental chambers without Collembola or nematodes. The number of *Galleria* still alive was determined after 24, 48, and 72 h by probing each larva with an applicator stick and recording those which responded.

Tests for Reduction of Nematode-induced Mortality of Galleria by Collembolan Predation

To determine how quickly predation by Collembola on *S. carpocapsae* could reduce nematodes-induced mortality of host larvae, samples (1 ml) containing an estimated 160 nematodes were added to each of 60 experimental chambers. One hundred *F. candida* were then added to 30 of the chambers. Ten *Galleria* were added to five chambers with Collembola and five without Collembola every 48 h for a total of 288 h. Mortality of *Galleria* was determined 48 h after they were introduced into the chambers.
The extent to which predation by varying densities of Collembola could limit nematode-induced mortality of *Galleria* was determined using four levels of *S. carpocapsae* (0, 50, 100, or 200) and six levels of *F. candida* (0, 5, 10, 20, 30, or 50) per chamber for a total of 20 treatments with five replicates of each. Suspensions of nematodes were introduced into the pre-moistened chambers, followed by the Collembola. Chambers were held in the dark at 24–25° for 24 h, after which ten *Galleria* larvae were added to each dish. Mortality of *Galleria* was determined after 48 h.

Tests for Reduction of Nematode-induced Mortality of P. japonica Grubs by Collembolan Predation

Experimental chambers were constructed by gluing the lid (7.3 cm outside diam [OD]) of a plastic jar (Cole-Palmer # 06101-30) inside one end of a piece of butyrate plastic tubing (10 cm length, 7.6 cm OD). Openings were cut in the lid (5.7 cm diam) and in the bottom (5.2 cm) of the jar. The jar was set in the bottom of a plastic petri dish, and a ring of C-PP poured around it.
Turfgrass plugs (6.3 cm diam) with underlying soil were cut from field plots of Kentucky bluegrass and inserted directly into the jars, producing a snug fit which limited the movement of Collembola between the sides of the jar and the soil. The lid was then placed over the jar with the open tubing extending upward. This arrangement confined the Collembola to the chambers without limiting air circulation, and made possible the addition of nematodes suspended in water, or additional irrigation water, with adequate drainage because the excess water was absorbed and then evaporated from the ring of C-PP.
Two trials were conducted using *F. candida* and Japanese beetle grubs, but with different species of entomopathogenic nematodes in each trial. For Trial 1, overwintering, third instar *P. japonica* were dug from Kentucky bluegrass turf on 27 January 1991. Ten replicates (chambers) of each of eight combinations of 0 or 2500 *S. carpocapsa* and 0, 100, 200, or 400 Collembola were prepared as follows. First, ten active *P. japonica* grubs were added to the top of the turfgrass plug within each chamber and allowed to burrow into the soil. Grubs that failed to bury themselves were replaced. Collembola and nematodes were then added to the appropriate chambers after 24 and 48 h, respectively. Nematodes were suspended in water, transferred by pipette, and spread evenly on the soil surface. The plugs were moistened with 0.5 cm (16 ml) of water before nematodes were applied. The chambers were held in a rearing room at 22 °C and a 16 : 8 h (L : D) photoperiod. Mortality of grubs was determined after 18 days.
Procedures were similar in Trial 2 except that *S. glaseri* were used. Third instar *P. japonica* were collected on 18 April and ten grubs were introduced into each turfgrass plug on the same day. Collembola (0 or 200) were added on 21 April, and nematodes (0, 575, 1150, 2300, or 4600) were added 24 h later. There were nine replicates for each treatment combination. Other procedures were as described for Trial 1.

Statistical Analyses

Data were analyzed by two sample t-tests or by standard analysis of variance (Anova) procedures using Statistic 3.5 Analytical Software, St. Paul, MN). Percentage data were arcsine transformed before analysis. In Trial 4 of the consumption tests (Section 2.1), ANOVA was followed by Dunnett's

multiple comparison test for treatments vs. control and linear contrasts were used to test for significance of effects of *F. candida* vs. *S. caecae*, and for linear effect of collembolan density on numbers of nematodes recovered. All data are presented as original means ± standard error (SE).

Results

Consumption of Nematodes by Collembola

Both species of Collembola readily consumed almost all of the *S. carpocapsae* when the insects were confined in chambers with exposed nematodes. *Folsomia cadida* also consumed large numbers of *S. feltiae*. Fewer, but significant numbers of *S. glaseri* also were consumed by both collembolan species (Table 1). Polynomial contrasts constructed separately for each collembolan species indicated a highly significant, negative linear relationship between density of Collembola and numbers of remaining nematodes for both *F. candida* ($F = 26.7$; $df = 3,12$; $P = 0.0002$) and *S. caeca* ($F = 74.0$; $df = 2,8$; $P < 0.0001$). At comparable densities (10 or 20 Collembola per chamber), *S. caeca* consumed significantly more *S. glaseri* than did *F. candida* (Anova, $P < 0.05$). In all trials the Collembola were still actively moving after exposure to nematodes, and some chambers had collembolan eggs present, indicating that the nematodes probably were not attacking the Collembola.

Tests for Phoresy of Nematodes on Collembola

No evidence of phoresy was detected. Nematodes were never observed attached to Collembola. No nematodes were recovered from Collembola by vigorous shaking of those that had been confined in chambers with nematodes. When Collembola were transferred from chambers with nematodes to new chambers with ten *Galleria* larvae, there was no significant increase in mortality of *Galleria* compared to that which occurred in control chambers which had never contained nematodes (96 vs. 98% survival, respectively, after 72 h). Similarly, there was high (96%) survival of *Galleria* larvae that were added to chambers that had been inoculated 6 days earlier with both *S. carpocapsae* and *F. candida.* However, when *Galleria* were added to chambers which had been inoculated 6 days earlier with *S. carpocapsae* alone, average survival rates were only 62, 20, and 10%, respectively, after 24, 48, and 72 h.

Tests for Reduction of Nematode-induced Mortality of Galleria by Collembolan Predation

Mortality of *Galleria* larvae caused by *S. carpocapsae* was inversely related to the length of time that the nematodes had been exposed to predation by *F. candida* (Fig. 1). Nearly all of the *Galleria* were killed in control dishes without Collembola, with little or no loss of infectivity of nematodes for at least 288 h. In contrast, mortality averaged 48% for *Galleria* added to chambers in which the nematodes had been exposed to collembolan predation for 48 h, declining to only 4% when Collembola had fed upon the nematodes for 288 h (Fig. 1). The effect of Collembola on mortality of *Galleria* was highly significant ($F = 264.7$; $df = 1.49$; $P < 0.0001$), with mortality declining linearly as the time of exposure of nematodes to Collembola increased (polynomial contrasts; $F = 23.4$; $df = 1.20$; $P < 0.001$).

In the second test, 100 or 200 *S. carpocapsae* caused high mortality of *Galleria* in the absence of Collembola, but addition of as few as five *F. candida* to the chambers for 24 h caused a significant reduction in nematode-induced mortality (Fig. 2). Overall effects were significant both for original nematode density ($F = 46.9$; $df = 5.72$; $P < 0.0001$) and

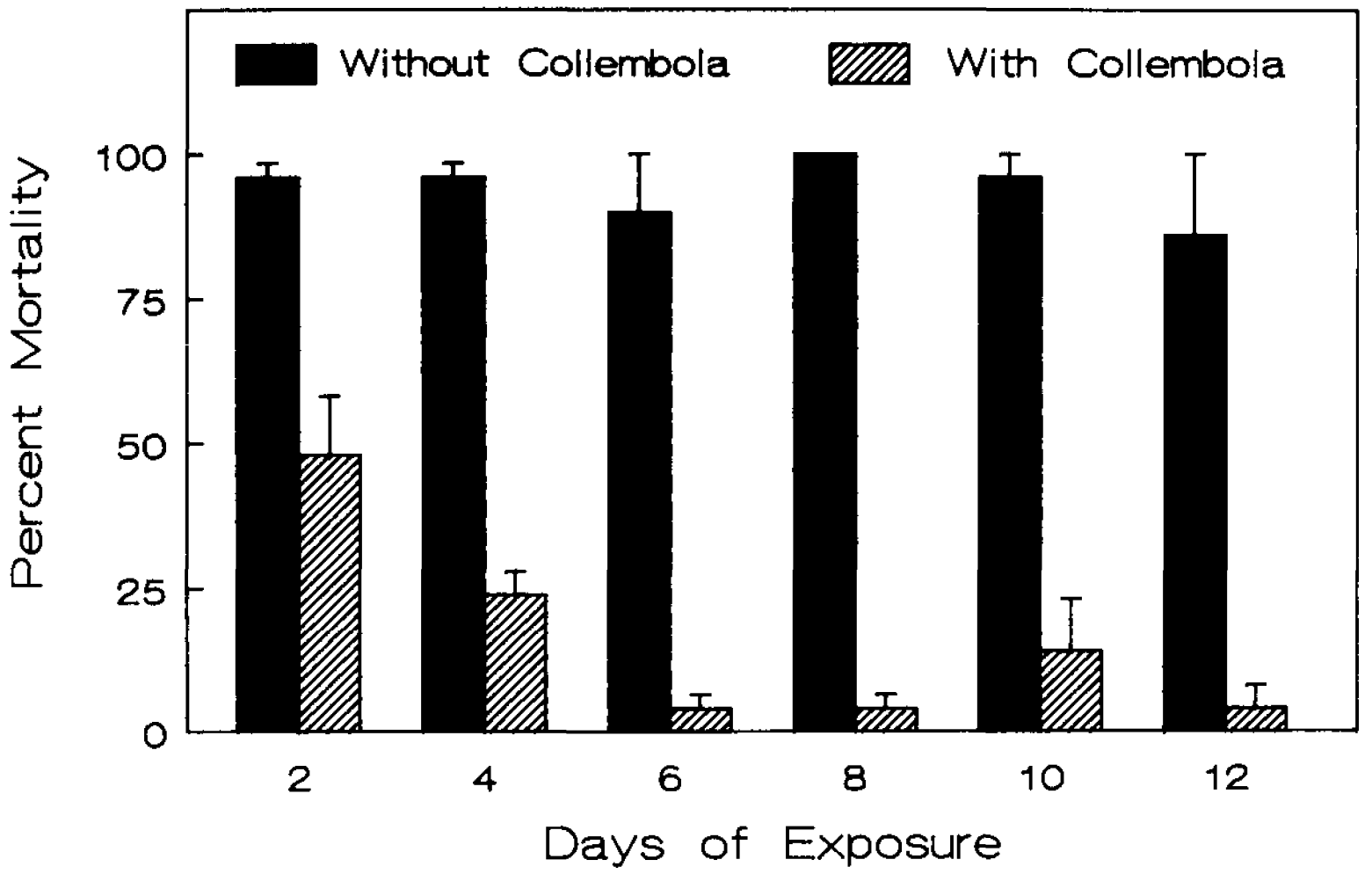

Fig. 1. Rate of reduction of wax moth larval mortality caused by *Steinernema carpocapsae* in the presence or absence of 100 *Folsomia candida*

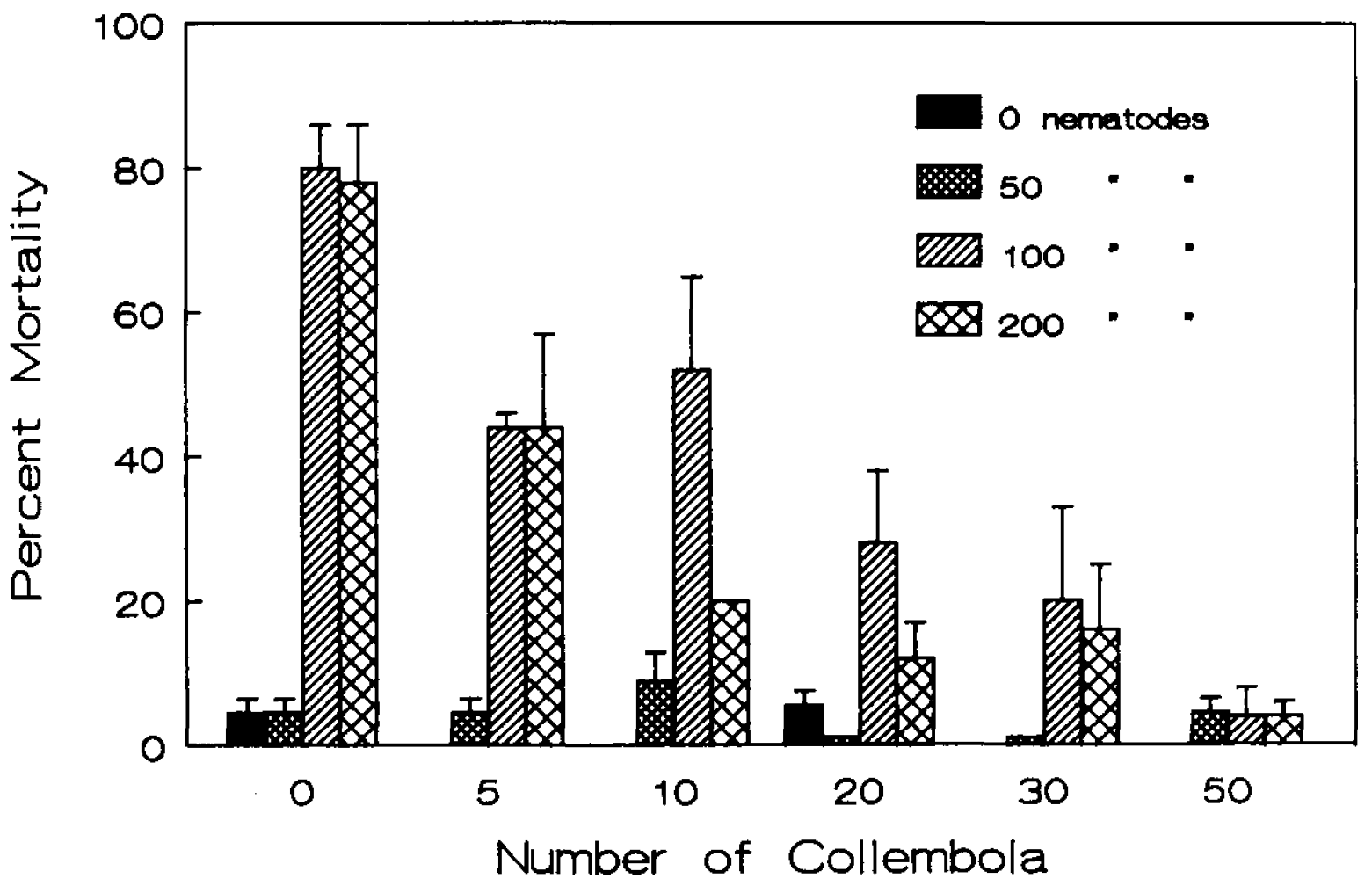

Fig. 2. Reduction in mortality of wax moth larvae in 48 h caused by different numbers of *Steinernema carpocapsae* in the presence or absence of varying densities of the collembolan *Folsomia candida*

Collembola density ($F = 16.37$; $df = 5.72$; $P < 0.001$). For chambers receiving 100 or 200 nematodes, mortality of *Galleria* decreased linearly with addition of increasing numbers of Collembola (polynomial contrasts; $F = 72.26$; $df = 1.48$; $P < 0.0001$).

Tests for Reduction of Nematode-induced Mortality of P. japonica Grubs by Collembolan Predation

In the first trial, treatment with 2500 *S. carpocapsae* failed to cause significant nematode-induced mortality of *P. japonica* grubs irrespective of whether or not varying numbers of the collembolan *F. candida* also were added. In the presence of 0, 100, 200, or 400

Collembola, mortality of grubs in nematode treated turf averaged 13, 18, 16, and 11%, respectively, compared with 15, 17, 18, and 12% mortality in turf plugs that were not treated with nematodes. Main effects were non-significant for presence or absence of nematodes ($F = 0.51$; $df = 1.63$; $p = 0.48$) and Collembola ($F = 1.04$; $df = 3.63$; $P = 0.38$). and there was no significant interaction ($F = 0.09$; $df = 3.63$; $P = 0.96$).
In the second trial, treatment with as few as 500 *S. glaseri* resulted in nearly complete mortality of *P. japonica* grubs. However, nematode-related mortality was not influenced by the presence and absence of 200 *F. candida*. Without Collembola present, mortality of *P. japonica* averaged 34.4 ± 15.0, 98.9 ± 3.1, 93.3 ± 15.6, 100, and 100% at nematode densities of 0, 500, 1000, 2000, and 4000, respectively. Corresponding mortality of grubs with Collembola also present averaged 35.6 ± 24.0, 98.9 ± 3.1, 100, 100, and 100%, respectively. Analysis of variance on arcsine-transformed percentages indicated a highly significant nematode effect ($F = 142.2$; $df = 4.72$; $P < 0.0001$) but no effect for Collembola ($F = 0.48$; $df = 1.72$; $P = 0.49$) and no Collembola by nematode interaction ($F = 0.66$; $df = 4.72$; $P = 0.63$).

Discussion

These tests demonstrated that some species of Collembola will consume large numbers of entomopathogenic nematodes, and that under laboratory conditions, collembolan predation is sufficient to interfere with nematode-induced mortality of *Galleria* larvae. Moreover, the Collembola tested were able to survive and reproduce in the presence of the nematodes. Many individuals produced eggs from which young hatched and developed through several molts (authors' observations). Nematodes were never observed to emerge from cadavers of Collembola that died during the tests, suggesting that mortality resulted from causes other than nematode infection.
Less clear, however, is the capacity for Collembolan predation to interfere with attempts to control subterranean pests of turfgrass or other commodities with entomopathogenic nematodes in the field. If the application is followed by irrigation, as is normally recommended (Shetlar et al., 1988; Georgis & Gaugler, 1991), the nematodes may enter the soil rapidly enough to escape significant collembolan predation on the soil surface.
Our test to determine if collembolan predation could reduce effectiveness of *S. carpocapsae* against *P. japonica* was inconclusive because of the nematodes' failure to cause significant mortality of grubs even in the absene of Collembola. Based upon analysis of multiple field trials, Georgis & Gaugler (1991) recently concluded that *S. carpocapsae* is ill-adapted to parasitize white grubs under any range of natural conditions. This is because of the nematode's tendency to remain near the soil surface (Georgis & Poinar, 1983a; Alatorre-Rosas & Kaya, 1990) coupled with its low host-finding ability (Choo et al., 1989).
In contrast, we found that *S. glaseri* caused high mortality of *P. japonica* grubs, but that it did so both in the presence and absence of *F. candida*. We speculate that the Collembola may have been unable to penetrate the relatively heavy Maury silt loam soil of the turfgrass plugs to feed upon nematodes below the surface. Vertical movement may vary among collembolan species, or be greater in soil with larger particles and more organic matter. Since the vertical movement of entomopathogenic nematodes is also affected by soil texture and composition (Georgis & Poinar, 1983a, b), the capacity for interaction between nematophagous Collembola and entomopathogenic nematodes may vary from site to site.
Although the two species of Collembola we tested were not found at the turfgrass site where the *P. japonica* larvae were collected, a related species, *Folsomia elongata* (MacGillivray) (Isotomidae) and other unidentified species were abundant. While different collembolans vary in their food preferences, a number of diverse species has been shown to consume nematodes (Gilmore, 1970). Given the seasonally fluctuating population patterns of Collembola (Usher, 1970; Takeda, 1976, 1983), and the fact that natural populations often exceed the densities used here (Christiansen, 1964; Tamura, 1976), we suggest that

collembolan predation could sometimes reduce the effectiveness of entomopathogenic nematodes in turfgrass, potting media, or other substrates.

Steinernema carpocapsae is more effective against pests such as sod webworms (Pyralidae), cutworms and armyworms (Noctuidae), and crane fly larvae (Tipulidae) that tunnel and feed at the soil-litter interface or on the soil surface than it is against subterranean white grubs (Shetlar 1989). We hypothesize that collembolan predation could have a greater effect on efficacy of *S. carpocapsae* against these pests. Following application, entomopathogenic nematodes may migrate across the soil surface before infecting a host (Poinar & Hom, 1986). Moreover, when third-stage juveniles emerge from a host cadaver, they may migrate over or through the soil or thatch to infect new hosts (Reed & Wallace, 1969). Collembolan predation on migrating nematodes could potentially limit the extension of control from the original host to secondary hosts.

The unpredictability of field applications has been a significant obstacle in expanding the successful use of entomopathogenic nematodes beyond their present limited markets (Georgis & Gaugler, 1991). It has become clear that physical factors such as soil type, temperature, irrigation frequency, and thatch depth can radically affect the efficacy of field releases (Georgis & Gaugler, 1991), but the effects of biotic factors on nematode survival and infectivity remain poorly known (Gaugler, 1988). Predation by Collembola may be an additional factor to be considered.

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